Atalanta (Mai 1992) **23**(1/2):195-214, Würzburg, ISSN 0171-0079

Egg surface morphology of Manioline butterflies

(Lepidoptera, Nymphalidae, Satyrinae)

by

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received 23.IX.1991

Abstract: The external morphology of ova of 14 species of the Satyrid tribe Maniolini was examined by scanning electron microscopy. The external morphology and chorion sculpturing of the ova is described. Intrageneric similarities, based on existing taxonomies, are reflected in the chorion form, although some species exhibit characters atypical of their genus. It is suggested that these differences are due to egg laying strategies and not to major evolutionary events.

Introduction

There are few detailed descriptions of the surface morphology of eggs of a closely related butterfly group based on scanning electron microscopy. Only the Satyrine genus *Melanargia* (EITSCHBERGER, STRÖHLE & WAGENER, 1986), the *Pieris napi-bryoniae* species complex (EITSCHBERGER, 1986) and some Nearctic Riodinidae and Lycaenidae have been tackled using this technique (DOWNEY & ALLYN, 1980a, b). Indeed, not all Manioline ova have been described from optical observations. There are no published descriptions of the ova of *Maniola megala*, *M. chia*, *M. telmessia*, *M. cypricola* or *M. halicarnassus*. For outline descriptions of the ova of species of Maniolini see HOWARTH (1973) for *jurtina*, *tithonus* and *hyperantus* and SIMMONDS (1930) for *nurag*. VILLA (1966) gives a detailed description of the ovum of *Pyronia cecilia*. A superficial description of the ova of *Hyponephele lupina* has been made by HESSELBARTH (1988). GILLMER (1900), DÖRING (1955), HESSELBARTH (1988) and FORSTER & WOHLFAHRT (1955) give varying descriptions of *lycaon* and HOWE (1975) gives an inadequate description of the ovum of *Cercyonis pegala*.

The tribe comprises five genera that have been defined on the basis of the structure of the male and female genital armature (DE LESSE, 1952). This paper describes the external morphology of all species of the genus *Maniola* (*jurtina* L. (1758), *megala* OBERTHÜR (1909), *chia* THOMSON (1987), *telmessia* ZELLER (1847), *halicarnassus* THOMSON (1990), *cypricola* GRAVES (1928) and *nurag* GHILIANI (1852)), most of the species of the genus *Pyronia* (*tithonus* L. (1771), *bathseba* FABRICIUS (1793) and *cecilia* VALLANTIN (1894)), *Aphantopus hyperantus* L. (1758), two of the species of the genus *Hyponephele* (*lycaon* KUHN (1774) and *lupina* COSTA (1836)) and the North American *Cercyonis pegala* FABRICIUS (1775). *Pyronia janiroides* HERRICH-SCHÄFFER (1852), *Hyponephele maroccana* BLANCHIER (1908), the Asiatic *Hyponephele* and the remaining species of the Nearctic genus *Cercyonis* were not available for this study.

Method and materials

Ova of all *Maniola* species, *Pyronia tithonus*, *P. bathseba*, *Aphantopus hyperantus* and *Hyponephele lycaon* were obtained from vagile wild caught females placed in 10 cm diameter ceramic pots. These contained a small amount of cut grass (species not identified), covered with black nylon netting. They were maintained in a controlled photo/thermoperiod environment (THOMSON, 1987). Ova from *Pyronia cecilia*, *Hyponephele lupina* and *Cercyonis pegala* were supplied by colleagues. Ova were taken from several adults to avoid the possibility that the females were aberrant individuals. When possible, eggs from five or more females of each species were utilised. The egg laying strategy (i.e. whether ova were fixed to a substrate or not) was noted in each species. The eggs were examined optically, by stereo microscope and by scanning electron microscope.

For electron microscopy, ova were mounted using double-sided adhesive tape. Conductive lacquer was applied liberally to the mount and tape. Specimens were given a light coating of gold using an Edwards S150 sputter coater. SEM work was performed on an ISI-60A instrument. All images were generated at 2.5 to 4kV.

Chorionic sculpturing of ova

A whole new taxonomy has been devised since the first electron microscope studies were published. In the following descriptions of the ova, the terminology used by ARBOGAST et al. (1980) has been followed.

Maniola jurtina (Figures 1, 15, 29)

Material examined: 10 ova from 5 females, Parma, Italy; 10 ova from 2 females, Vienna, Austria; 10 ova from 2 females, Easdale Island, Argyll; 10 ova from 2 females, Kinvara, Co. Clare; 10 ova from 2 females, Head of Holland, Orkney.

Ova subspherical to truncated conical, tapering slightly to anterior pole. Longitudinal ribs 18 to 21, distinct. Transverse ribs fine, sinuous, usually incomplete.

Aeropyles numerous, located on the longitudinal rib apices, collars low or absent.

Anterior zone comprised of two distinct regions of primary and secondary cells, separated and bounded outwardly by distinct concentric ridges, formed of subparallel intersecting subridges. A third concentric tertiary cell region lies outwith the secondary cell ring, indistinctly separated from and forming part of the longitudinal/transverse rib zone.

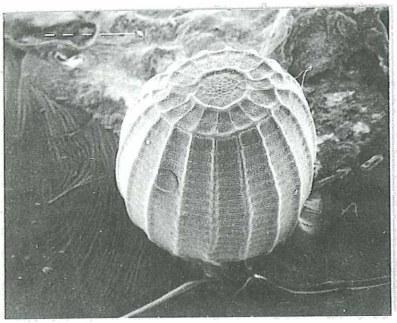
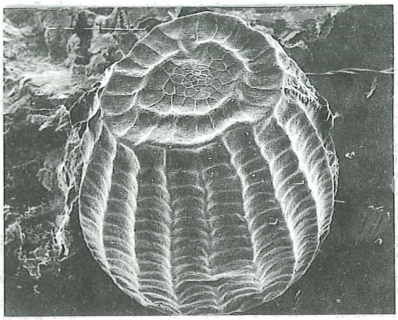
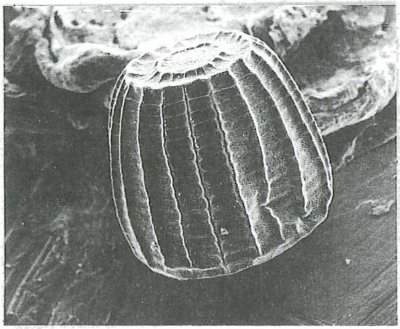
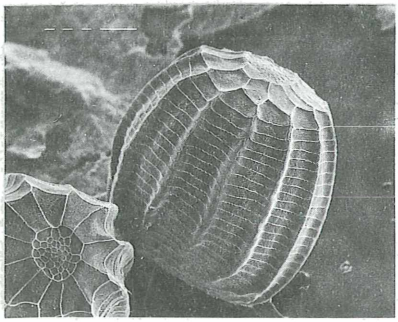
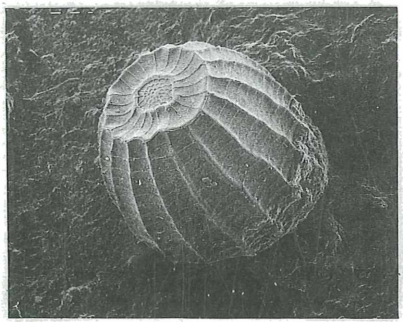
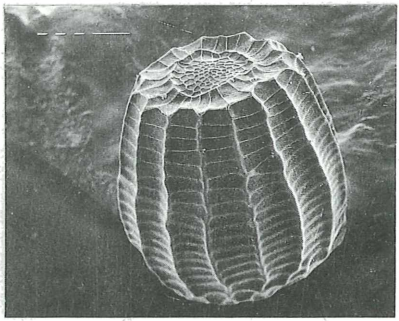
Micropylar canals two to four in number, set in a deep micropylar pit, surrounded by a rosette of three to six petal shaped primary cells, defined by distinct ridges. Other primary cells polygonal, complex, forming a web-like pattern. Ribs dividing secondary cells approximately similar to longitudinal ribs in number.

Chorion surface reticulate, covered with adjacent, irregularly shaped polygonal prominences.

Maniola megala (Figures 2, 16, 30)

Material examined: 25 Ova from 3 females, Marmaris, Turkey.

Ova subspherical to truncated conical, tapering to anterior pole: taller than *jurtina* ova. Longitudinal ribs 19 to 21, distinct. Trans verse ribs more distinct than in *jurtina*, usually complete.

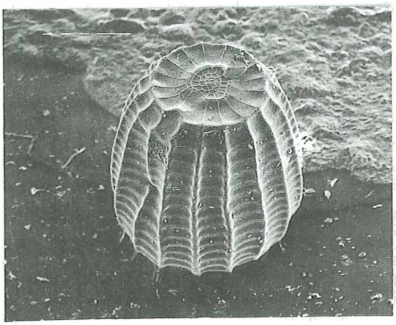
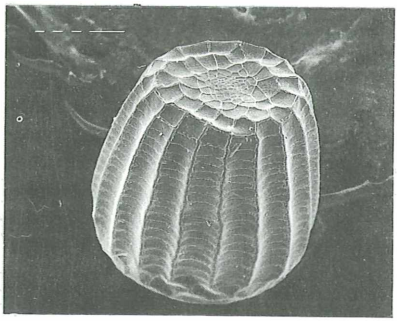
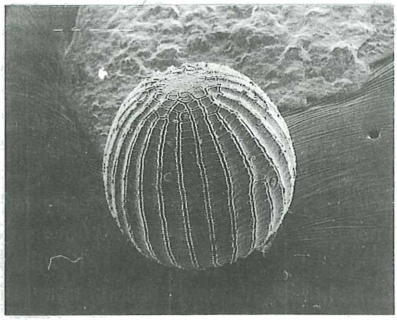
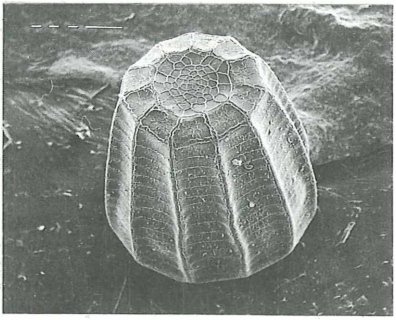
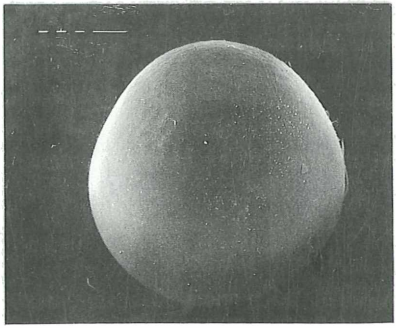
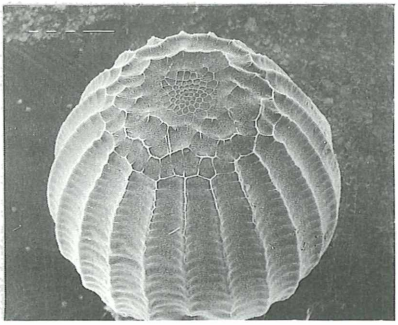







1	2
4	3
5	6

1) *Maniola jurtina* 2) *Maniola megala*

3) *Maniola chia* 4) *Maniola telmessia*

5) *Maniola halicarnassus* 6) *Maniola cypricola*

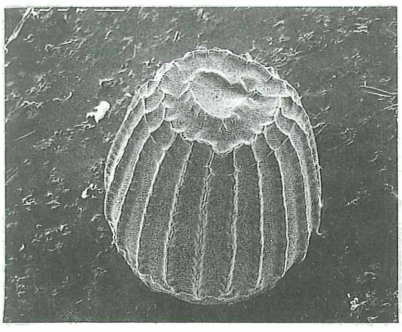
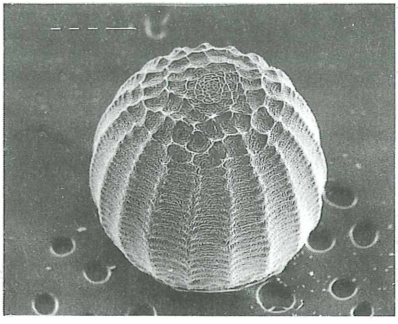
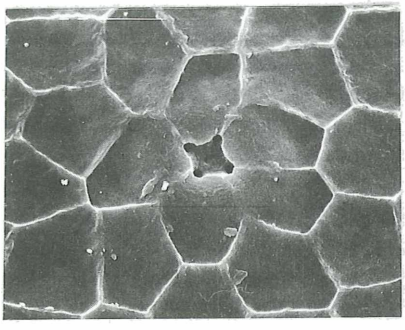
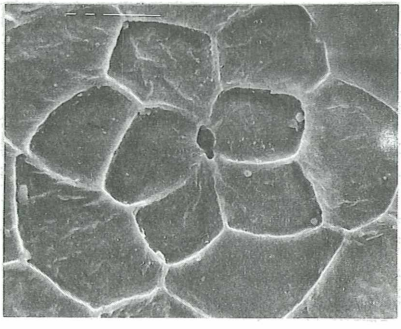
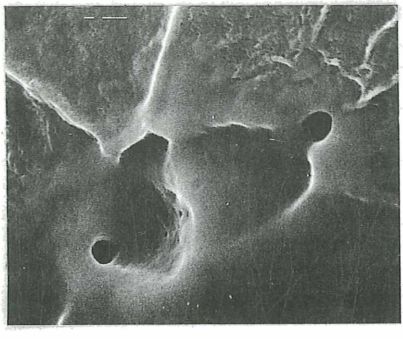
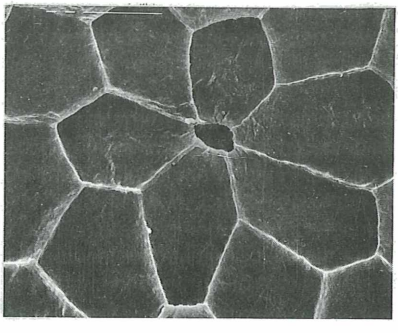







7	8
9	10
11	12

7) *Maniola nurag* 8) *Pyronia tithonus*

9) *Pyronia bathseba* 10) *Pyronia cecilia*

11) *Aphantopus hyperantus* 12) *Hyponephele lycaon*

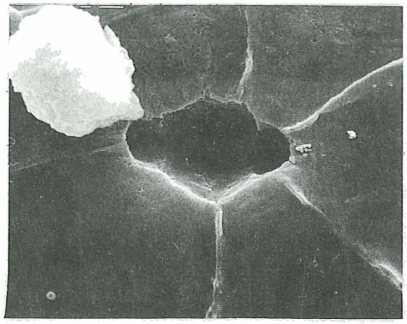
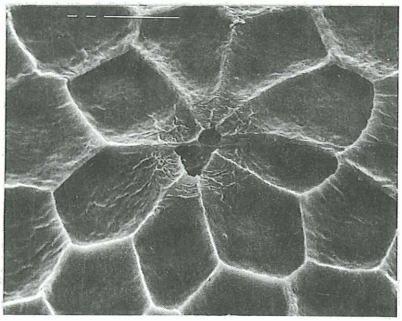
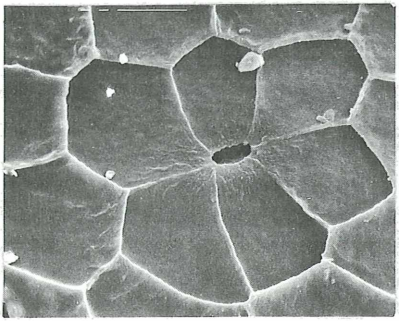
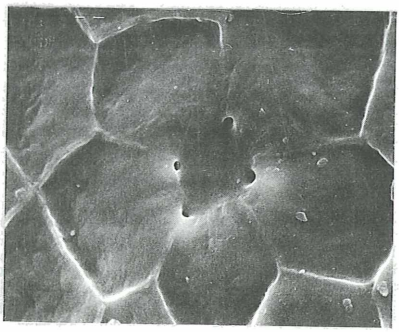
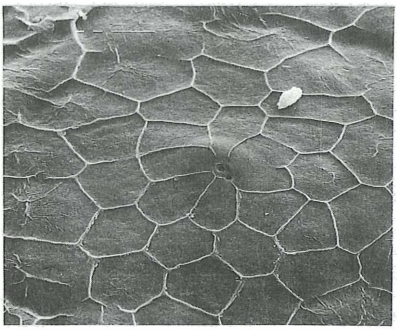
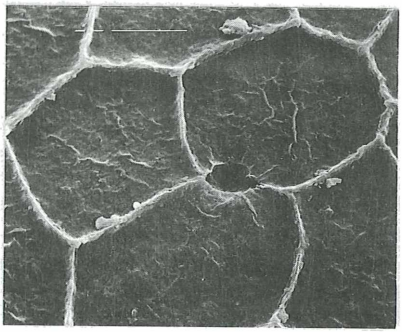







13	14
15	16
17	18

13) *Hyponephele lupina* 14) *Cercyonis pegala*

15) *Maniola jurtina* 16) *Maniola megala*

17) *Maniola chia* 18) *Maniola telmessia*

19	20
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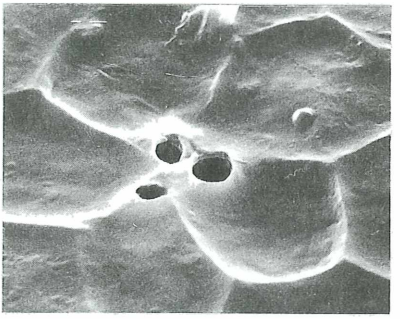
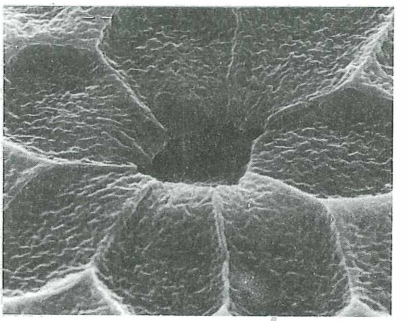
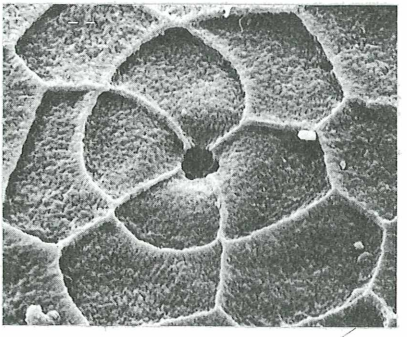
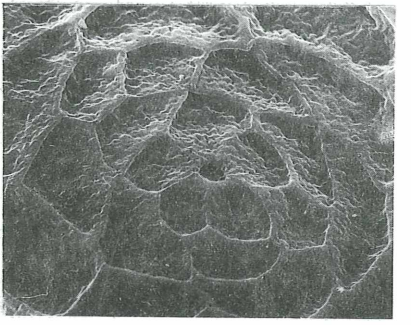
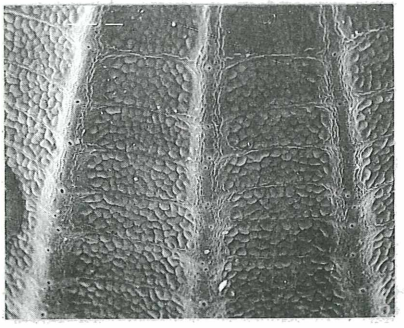
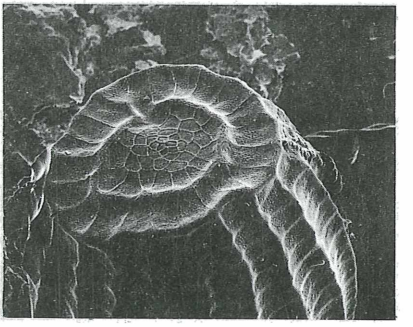
19) *Maniola halicarnassus* 20) *Maniola cypricola*

21) *Maniola nurag* 22) *Pyronia tithonus*

23) *Pyronia bathseba* 24) *Pyronia cecilia*

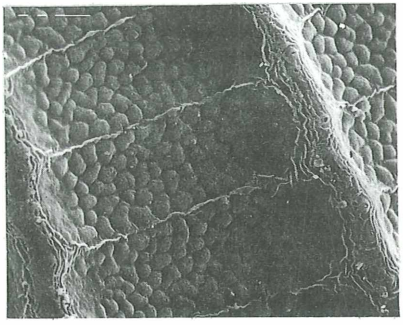
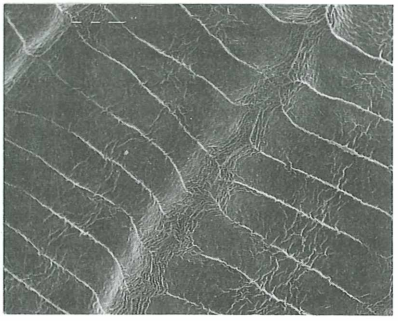
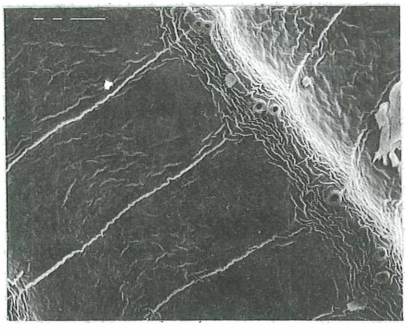
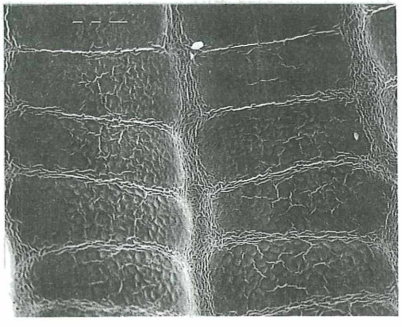
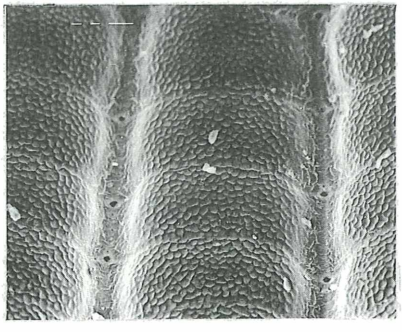
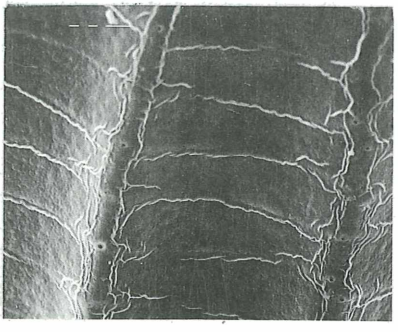







25	26
27	28
29	30

25) *Aphantopus hyperantus* 26) *Hyponephele lycaon*

27) *Hyponephele lupina* 28) *Cercyonis pegala*

29) *Maniola jurtina* 30) *Maniola megala*

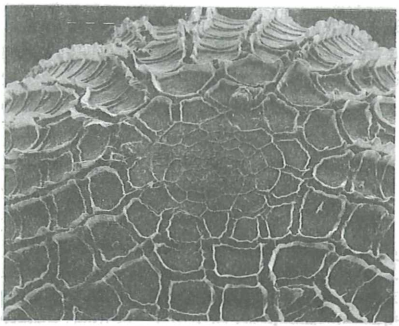
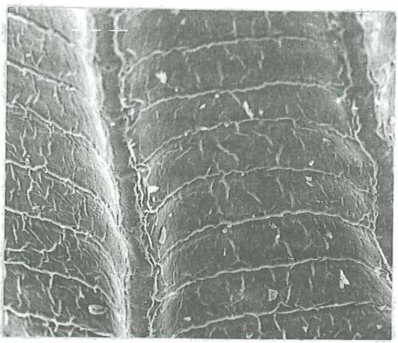
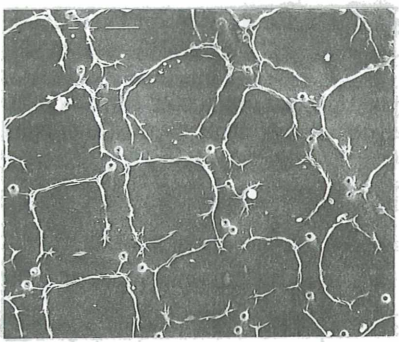
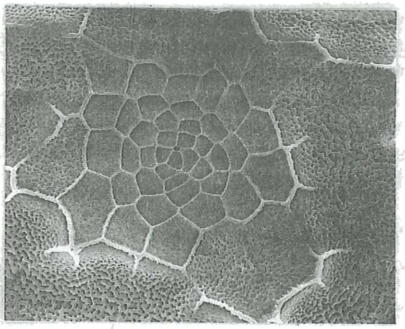
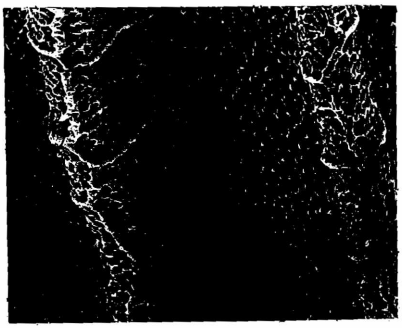
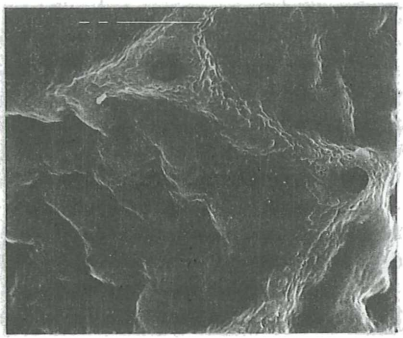







31	32
33	34
35	36

31) *Maniola chia* 32) *Maniola telmessia*

33) *Maniola halicarnassus* 34) *Maniola cypricola*

35) *Maniola nurag* 36) *Pyronia tithonus*

37	38
39	40
41	42

37) *Pyronia bathseba* 38) *Pyronia cecilia*

39) *Aphantopus hyperantus* 40) *Hyponephele lycaon*

41) *Hyponephele lupina* 42) *Cercyonis pegala*

Aeropyles numerous, located on the longitudinal rib apices, collars low or absent.
Anterior zone similar to *jurtina*, concentric ridges rather higher.
Micropylar canals two to four in number, set in a deep micropylar pit, surrounded by a rosette of five petal shaped primary cells, defined by distinct ridges. Other primary, secondary and tertiary cells similar to *jurtina*.
Chorion surface like *jurtina*.

Maniola chia (Figures 3, 17, 31)

Material examined: 11 ova from 1 female, Nea Moni, Chios.

Ova subspherical to truncated conical, tapering slightly to anterior pole, shorter than *jurtina* or *megala*. Longitudinal ribs 13 to 14, distinct. Transverse ribs fine, sinuous, usually incomplete.
Aeropyles numerous, located on the longitudinal rib apices, collars low or absent.
Anterior zone similar to *jurtina*, but tertiary cell region even less distinctly separated from the longitudinal/transverse rib zone.
Micropylar canals two to four in number, set in a deep micropylar pit, surrounded by a rosette of three to six petal shaped primary cells, defined by distinct ridges. Other primary, secondary and tertiary cells similar to *jurtina*.
Chorion surface like *jurtina*.

Maniola telmessia (Figures 4, 18, 32)

Material examined: 5 ova from 1 female, Hakkari, Turkey; 15 ova from 1 female, Antalya, Turkey.

Ova barrel shaped to truncated conical. Longitudinal ribs 14 to 16, prominent. Transverse ribs distinct, complete.
Aeropyles numerous, located on the longitudinal rib apices, collars distinct.
Anterior zone comprised of primary, secondary and tertiary cell regions as *jurtina*. Primary and secondary regions separated by a prominent concentric ridge. Ridge separating secondary and tertiary regions usually less prominent.
Micropylar canals four in number, set in a deep micropylar pit, surrounded by a rosette of four to six petal shaped primary cells, defined by distinct ridges. Other primary and secondary cells fewer in number than *jurtina*.
Chorion surface sparsely covered with low prominences and fine, sinuous, irregular ridges: ridges most frequent in secondary cell region and in the interlongitudinal rib depressions.

Maniola halicarnassus (Figures 5, 19, 33)

Material examined: 10 ova from 2 females, Bodrum, Mugla Province, Turkey; 20 ova from 2 females, Nisyros, Greece.

Ova barrel shaped to truncated conical. Longitudinal ribs 9 to 18, prominent (as telmessia). Transverse ribs distinct, sinuous and complete.
Aeropyles numerous, located on the longitudinal rib apices, collars distinct.
Anterior zone comprised of primary and secondary cell regions. Tertiary cell region almost indistinguishable.

Micropylar canals two to three in number, set in a deep micropylar pit, surrounded by a rosette of five to seven petal shaped primary cells, defined by very distinct ridges. Other primary cells similar to *telmessia*.
Chorion surface similar to *telmessia*.

Maniola cypricola (Figures 6, 20, 34)

Material examined: 15 ova from 5 females, Paphos, Cyprus.

Ova barrel shaped to truncated conical. Longitudinal ribs 13 to 14, prominent (as *telmessia*). Transverse ribs distinct, sinuous and complete.
Aeropyles numerous, located on the longitudinal rib apices, collars distinct.
Anterior zone comprised of primary and secondary cell regions. Tertiary cell region indistinguishable.
Micropylar canals two to three in number, set in a deep micropylar pit, surrounded by a rosette of eight petal shaped primary cells, defined by very distinct ridges. Other primary cells more numerous than in other *Maniola* species.
Chorion surface similar to *telmessia*.

Maniola nurag (Figures 7, 21, 35)

Material examined: 6 ova from 1 female, Correboi, Sardinia.

Ova barrel shaped. Longitudinal ribs 16 to 17, prominent. Transverse ribs low, complete, not sinuous as in other *Maniola*.
Aeropyles located only at the junctures of the longitudinal and transverse ribs, collars distinct.
Anterior zone comprised of primary, secondary and tertiary cell regions.
Micropylar canals two in number, set in a deep micropylar pit, surrounded by a rosette of six petal shaped primary cells, defined by very distinct ridges. Other primary and secondary cells fewer in number than other *Maniola* species.
With the exception of primary, secondary and tertiary cell regions, chorion surface reticulate, covered with low polygonal prominences. Primary cell area irregularly sinuous. Secondary and tertiary cell regions with numerous sinuous ridges.

Pyronia tithonus (Figures 8, 22, 36)

Material examined: 30 ova from 6 females, St Bees, Cumbria.

Ova barrel shaped, tapering along whole length to anterior pole. Longitudinal ribs 16, prominent. Transverse ribs fine, sinuous, usually complete.
Aeropyles numerous, located on the longitudinal rib apices, collars low or indistinct.
Anterior zone indistinctly divided into primary and secondary cell regions, separated and bounded by distinct single or double ridges. Concentric region of tertiary cells indistinctly separated from the longitudinal/transverse rib zone.
Micropylar canals four in number, set in a shallow, indistinct micropylar pit, surrounded by a rosette of five petal shaped primary cells, outwardly defined by distinct ridges. Other primary cells numerous, complex, forming a web-like pattern. Ribs dividing secondary cells approximately similar to longitudinal ribs in number.

Chorion surface indistinctly reticulate, covered with irregularly shaped prominences.

Pyronia bathseba (Figures 9, 23, 37)

Material examined: 15 ova from 5 females, Fountain de Vaucluse, France; 10 ova from 1 females, Madrid, Spain; 10 ova from 1 female, Guadalajara, Spain.

Ova spherical to subspherical. Longitudinal ribs 22, distinct, and formed of paired, parallel, membranous ridges. Transverse ribs less distinct than longitudinal ribs, similarly formed.
Aeropyles absent or undetected.
Anterior zone comprised of a single area of primary and (possibly) secondary cells, defined by single distinct ridges.
Micropylar canals two in number, set in a shallow, distinct micropy lar pit, surrounded by a rosette of five to six petal shaped primary cells, defined by distinct ridges. Secondary cells merge into longitudinal/transverse rib zone.
Chorion surface smooth.

Pyronia ceciiia (Figures 10, 24, 38)

Material examined: 10 ova from 2 females, Nuoro, Sardinia.

Ova truncated conical, sides straight or concave. Longitudinal ribs 10 to 12, very prominent. Transverse ribs fine, sinuous and complete.
Aeropyles present only at the junctures between longitudinal and transverse ribs, collars distinct.
Anterior zone slightly concave, flat or slightly convex (possibly dependent upon age and/or desiccation), divided very distinctly into primary and secondary cell regions by prominent concentric ridges.
Micropylar canals two (possibly up to five) in number, set in a deep micropylar pit, surrounded by a rosette of four or five petal shaped primary cells. Other primary cells numerous, complex forming a web-like pattern. Ribs defining secondary cells of the same number as longitudinal ribs.
Chorion surface covered with fine sinuous, irregular and incomplete ridges.

Aphantopus hyperantus (Figures 11, 25, 39)

Material examined: 20 ova from 5 females, Gignod, Italy; 30 ova from 5 females, Doune, Perthshire.

Ova spherical to subspherical, tapering slightly to anterior pole. Longitudinal and transverse ribs detectable only as subregular patterns of sinuous, paired, parallel ridges on barely distinguishable, very slightly raised ribs.
Aeropyles present over whole chorion surface, collars distinct.
Anterior zone detectable only as a very slight depression, not clearly divided into primary and secondary cell regions.
Micropylar canals three in number, not set in a micropylar pit, surrounded by a very indistinct rosette of petal shaped primary cells. Ridges low or absent. Secondary cells, when detectable, with low, single ridges.
Chorion surface smooth.

Hyponephele lycaon (Figures 12, 26, 40)

Material examined: 20 ova from 5 females, Monti Sibillini, Italy.

Ova spherical. Longitudinal ribs 21, prominent. Transverse ribs numerous, low and detectable only at their junctures with the longi tudinal ribs.
Aeropyles numerous, collars indistinct.
Anterior zone comprised of two regions of primary and secondary cells.
Micropylar canals three in number, set in a deep micropylar pit, surrounded by a rosette of five to seven petal shaped primary cells, defined by prominent ridges. Other primary cells polygonal, complex, increasing in size radially. Secondary cells incomplete, partially defined by distinct ridges.
Chorion surface deeply pitted over whole surface, except primary cell area. Primary cell area irregularly and deeply wrinkled.

Hyponephele lupina (Figures 13, 27, 41)

Material examined: 8 ova from 1 female, near Oran, Ankara, Turkey; 12 ova from 4 females, Rogues, Gard, France; 10 ova from 2 females, Moni Kykes, Cyprus.

Ova subspherical to subcylindrical. Longitudinal ribs 17-20, prominent. Transverse ribs numerous, low but almost complete.
Aeropyles numerous, collars indistinct.
Anterior zone comprised of two very distinct regions of primary and secondary cells by prominent concentric ridges. Concentric region of tertiary cells very indistinctly separated from the longitudinal transverse rib zone.
Micropylar canals three to eight in number, set in a deep micropylar pit, surrounded by a rosette of five or six petal shaped primary cells, defined by prominent ridges. Other primary cells polygonal, complex, increasing in size radially. Secondary cells defined by distinct ribs, complete and of the same number as longitudinal ribs.
Chorion surface deeply pitted over whole surface, except primary cell area. Inner cells of primary cell area irregularly wrinkled, outer cells pitted.

Cercyonis pegala (Figures 14, 28, 42)

Material examined: 10 ova from 2 females, Macombe, Illinois, USA.

Ova spherical. Longitudinal ribs 18, prominent. Transverse ribs numerous, low and detectable only at their junctures with the longi tudinal ribs.
Aeropyles numerous, collars indistinct.
Anterior zone comprised of two illdefined regions of primary and secondary cells.
Micropylar canals two in number, set in a very deep micropylar pit, surrounded by a rosette of four petal shaped primary cells, defined by very prominent ridges. Secondary cells incomplete, outwardly defined by prominent ridges.
Chorion surface, including primary cell area, entirely covered with a complex series of deep, convoluted rib-like structures.

The principal character state differences described above are summarised in table 1.

Table 1: Principal character states of chorionic sculpturing in ova of Maniolini.

species	shape	longitudinal ribs	transverse ribs	anterior zone areas	micropyle canal number	primary cell petals	surface
jurtina	subcylindrical to truncated conical	18-21/ distinct	fine incomplete sinuous	3	2-4	3-6	polygonal prominences
megala	subcylindrical to truncated conical	19-21/ distinct	fine complete sinuous	3	2-4	5	polygonal prominences
chia	subcylindrical to truncated conical	13-14/ distinct	fine incomplete sinuous	3	2-4	3-6	polygonal prominences
telmessia	barrel shaped to truncated conical	14-16/ prominent	distinct complete sinuous	3	4	4-6	polygonal prominences + sinuous ribs
halicarnassus	barrel shaped to truncated conical	9-18/ prominent	distinct complete sinuous	2-3	2-3	5-7	polygonal prominences + sinuous ribs
cypricola	barrel shaped to truncated conical	13-14/ prominent	distinct complete sinuous	2	3	8	polygonal prominences + sinuous ribs
nurag	barrel shaped	16-17/ prominent	low complete not sinuous	2	2	6	polygonal prominences + sinuous ribs
tithonus	barrel shaped	16/ prominent	fine complete sinuous	3	4	5	polygonal prominences
bathseba	spherical to subspherical	20/ distinct	distinct paired sinuous	2	2	5-6	smooth
cecilia	truncated conical	10-12/very prominent	fine complete sinuous	2	2 (-5)	5	
hyperantus	spherical	very indistinct (? absent)	very indistinct	1	3	0	smooth
lycaon	spherical	21/ prominent	low incomplete	2	3	5-7	pitted
lupina	subspherical to subcylindrical	17-20/ prominent	low complete	2-3	3-8	5-6	pitted
pegala	spherical	18/ prominent	low incomplete	1-2	2	4	deeply wrinkled

Other observations

Most eggs were laid on the net covering the pots, although a significant number was laid on the pot sides. Few eggs were deposited on grass. Oviposition strategy is listed in table 2, although these observations must be treated only as tentative, as oviposition in the wild state may differ from that in captivity (CHEW & ROBBINS, 1984).

Table 2: Oviposition strategy of Maniolini in captivity: degree of ova adhesion to foodplant or other substrate.

	very firm	firm	light	very light	not fixed
Maniola jurtina			*	*	
Maniola megala			*	*	
Maniola chia			*	*	
Maniola telmessia			*		
Maniola halicarnassus			*		
Maniola cypricola			*		
Maniola nurag			*		
Pyronia tithonus					
Pyronia bathseba					
Pyronia cecilia					
Aphantopus hyperantus					
Hyponephele lycaon					
Hyponephele lupina					
Cercyonis pegala					

Little importance is placed on size differences which were noted between closely related species. BRAKEFIELD (1979) suggests that the size of *jurtina* ova decreases northwards through Europe. However, many factors can contribute to ovum size differences (KARLSSON & WIKLUND, 1985), including adult age and imaginal nutrition (TELFER & RUTBERG, 1960), although the interactions of nutritional factors and endrocrinology in butterflies are not well understood (TOJO et al., 1981). Variation in egg size in Lepidoptera probably is the norm (ARBOGAST et al., 1980). In the present study it was found that ovum size varied in most species, with a marked tendency for size to increase as oviposition progressed. There was a slight decrease in size at the end of the oviposition period. This is in contrast with the observations of JONES et al. (1982) who noted that eggs produced by individuals became smaller as females aged. BRAKEFIELD's data were based on weight, but KARLSSON & WIKLUND (1985) have shown that this parameter is an invalid measure of egg size. In the present work egg sizes were assessed subjectively and precise measurements of intraspecific variation were not made.

Variation in longitudinal rib (keel) number was recorded in most *Maniola* species in ova laid be the same female. DENNIS & RICHMAN (1985) noted that ova with eight and nine keels were found in single batches laid by *Aglias urticae*. However, they could not be absolutely certain if they were the offspring from one or more females. Rib number on eggs laid by ten females of *halicarnassus* from the Greek Island of Nisyros were counted. Half the parents laid eggs with 16 ribs, while the other half laid eggs with varying rib numbers. These ranged from 9 to 16 from the same females, although the majority had 16. Interestingly, the rib number appeared to stabilise as egg laying progressed. Similar variation was noted in the same species from Bodrum (THOMSON, 1990). It is presumed that the gross architecture of the ova is determined in the progressively enlarging and maturing follicles within the ovarioles, and certainly before the eggs reach the oviduct (STERN & SMITH, 1960; EHRLICH & EHRLICH, 1978; DUNLAP-PIANKA, 1979; HINTON, 1981, HERMAN & DALLMAN, 1981). No explanation can be suggested at present for such variation in longitudinal rib number. However, this phenomenon appears to be the norm in Maniolini and might be widespread throughout Lepidoptera. Care must be taken in its interpretation.

Asymmetry in overall form was noted in *M. cypricola* and *H. lycaon*.

Differences in ova colouration were of little significance in the present context. *Maniola* and *Pyronia* ova are irregularly speckled light and dark brown, with extensive individual and geographical variation. The more macular markings on *cypricola* ova are distinct from those on ova of the other *Maniola* species. *Aphantopus*, *Hyponephele* and *Cercyonis* ova are uniformly pale yellow/grey.

Significant geographical variation was noted only in *H. lupina*. The subspherical ova from France and Cyprus are very different from the subcylindrical ova from Turkey. The number of micropylar canals is greater in French and Cypriot *lupina* ova. These differences correspond to large genetic differences between similar populations detected by electrophoresis (THOMSON, 1987).

Discussion

It is shown here that chorionic sculpturing, revealed by scanning electron microscopy, is a valuable indicator of evolutionary relationships in Maniolini. The complex morphology of these ova suggests relation ships that agree with accepted systematic arrangements, although the ova of *Pyronia tithonus* are remarkably similar to those of *Maniola* species, and much closer to them than to its congeners. Ova of *Maniola* are very similar to each other, with only minor, although important, differences in ribbing and ultrastructure. *Hyponephele* and *Cercyonis* ova have similarities that suggest close affinity. The simple, spherical ova of *Aphantopus* are unique in the group, although the structure of the ribs, when present, is similar to those of *bathseba* ova. Interspecific differences between *Pyronia* ova are greater than between species in other genera.

DE BEER (1958) observes that evolutionary affinities between major groups of animals are frequently manifest in embryonic stages of the organisms. This is often not so in Lepidoptera, in which convergence in the immature insects is commonplace (MILLER, 1968). Behavioural differ ences, which might or might not have phylogenetic significance, can contribute towards the evolution of differential shape and form. In Manioline ova, for example, the egg-laying strategy of *Pyronia bathseba* and *Aphantopus hyperantus*, which distribute

their eggs freely with little or no adhesion to the larval hostplant (FORSTER & WOHLFAHRT, 1955) is markedly different from that of the congeneric species, *Pyronia cecilia*, which fix their eggs firmly (VILLA, pers. comm.). The general chorionic architecture, therefore, is not necessarily a consequence of the major evolutionary processes.

It is suggested that these large intrageneric differences in *Pyronia* and occasional transgeneric similarities in ova morphology (between *Maniola* species and *Pyronia tithonus*, and between *Pyronia bathseba* and *Aphantopus hyperantus*) are a consequence of oviposition strategy. Sometimes selection associated behavioural adaptations of this sort are so great (as in *Pyronia*) that they appear to contribute to changes in the expected genetically determined archetype. Although not a direct corollary of this hypothesis, it is worth noting that the mechanism for similar evolutionary events, in the form of large 'jumps' to alternative foodplants, was proposed by CHEW & ROBBINS (1984). However, some features of the ova must be determined genetically. The relationships between *jurtina*, *megala* and *chia* and between *telmessia*, *halicarnassus*, *cypricola* and *nurag* can be seen in characteristics of the chorionic ultrastructure, while evolutionary affinities must be inferred from the very similar ova ultrastructure in *Hyponephele* and *Cercyonis*, genera found in two continents separated by several thousand kilometres.

Acknowledgements

I have to thank Dr. DAVID BRYANT and the University of Stirling for access to equipment and facilities, especially the scanning electron microscope, TOM FOREST and JAMES PURVIS who assisted with scanning electron microscopy and LEWIS TAYLOR who undertook the film processing. I also thank ROBERT PARKER, Dr. ROBERTO VILLA, GERHARD HESSELBARTH, ALAIN OLIVIER and Dr. ENRIQUE GARCIA-BARROS who supplied live females or ova.

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Figures 1-14

Scanning electron micrographs of Manioline ova.

1 *Maniola jurtina*, Dunblane, Perthshire, X85, SEM0540/3
2 *M. megala*, Marmaris, Turkey, X110, SEM0580/2
3 *M. chia*, Chios, Greece, X87, SEM0644/2
4 *M. telmessia*, Hakkari, Turkey, X91, SEM0578/12
5 *M. halicarnassus*, Nisyros, Greece, X90, SEM0662/13
6 *M. cypricola*, Episkopi, Cyprus, X91, SEM0500/1
7 *M. nurag*, Correboi, Sardinia, X85, SEM0532/9
8 *Pyronia tithonus*, St Bees, Cumbria, X87, SEM0558/12
9 *P. bathseba*, Madrid, Spain, X63, SEM0593/7
10 *P. cecilia*, Nuoro, Sardinia, X90, SEM0511/2
11 *Aphantopus hyperantus*, Doune, Perthshire, X83, SEM0495/8
12 *Hyponephele lycaon*, Planet, Italy, X78, SEM0420/7
13 *H. lupina*, Rogues, France, X74, SEM0663/1
14 *Cercyonis pegala*, Macomb, USA, X73, SEM0457/5

Figures 15-28

Scanning electron micrographs of Manioline ova - micropyle area.

15 *Maniola jurtina*, Dunblane, Perthshire, X1790, SEM0540/5
16 *M. megala*, Marmaris, Turkey, X1410, SEM0582/4
17 *M. chia*, Chios, Greece, X6000, SEM0645/4
18 *M. telmessia*, Hakkari, Turkey, X1970, SEM0573/6
19 *M. halicarnassus*, Bodrum, Turkey, X6100, SEM0653/1
20 *M. cypricola*, Episkopi, Cyprus, X1910, SEM0505/7
21 *M. nurag*, Correboi, Sardinia, X1790, SEM0534/7
22 *Pyronia tithonus*, St Bees, Cumbria, X2600, SEM0551/4
23 *P. bathseba*, Fountain de Vaucluse, France, X730, SEM0406/1
24 *P. cecilia*, Nuoro, Sardinia, X1910, SEM0515/7
25 *Aphantopus hyperantus*, Doune, Perthshire, X4100, SEM0498/11
26 *Hyponephele lycaon*, Planet, Italy, X5000, SEM0418/4
27 *H. lupina*, Ankara, Turkey, X1900, SEM0654/3
28 *Cercyonis pegala*, Macomb, USA, X1500, SEM0454/3

Figures 29-42

Scanning electron micrographs of Manioline ova - rib structure.

29 *Maniola jurtina*, Dunblane, Perthshire, X430, SEM0539/2
30 *M. megala*, Marmaris, Turkey, X220, SEM0586/9
31 *M. chia*, Chios, Greece, X880, SEM0648/7
32 *M. telmessia*, Hakkari, Turkey, X390, SEM0570/2
33 *M. halicarnassus*, Bodrum, Turkey, X870, SEM0650/10
34 *M. cypricola*, Episkopi, Cyprus, X450, SEM0501/2
35 *M. nurag*, Correboi, Sardinia, X610, SEM0530/2
36 *Pyronia tithonus*, St Bees, Cumbria, X620, SEM0530/2
37 *P. bathseba*, Madrid, Spain, X250, SEM0595/10
38 *P. cecilia*, Nuoro, Sardinia, X440, SEM0512/4
39 *Aphantopus hyperantus*, Doune, Perthshire, X830, SEM0491/2
40 *H. lycaon*, Planet, Italy, X400, SEM0422/10
41 *H. lupina*, Ankara, Turkey, X800, SEM0656/7
42 *Cercyonis pegala*, Macomb, USA, X2120, SEM0455/2

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